

ANALYSIS OF MULTIPLE CAPTURE-RECAPTURE
DATA USING BAND-RECOVERY METHODS

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SUMMARY

One simple approach to the analysis of multiple capture-recapture data is to use only first and last captures and carry out the band-recovery analyses of Brownie *et al.* (1978). In this paper, we present the loss in efficiency of this approach compared to the Jolly-Seber analysis and its age-dependent extension. We also develop estimates of capture probabilities and population sizes for the first and last capture data. Finally, we present an example from the fossil record where only first and last capture data are available, so that the Jolly-Seber model cannot be used.

1. Introduction

Procedures for the statistical analysis of band or tag return data which are described in a handbook by Brownie *et al.* (1978) are now being widely used by wildlife and fisheries biologists. This is due in part to the availability of supporting computer software from the U. S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland.

Brownie *et al.* (1978) suggest that until analogous methodology involving a comparable series of models is developed for live or multiple recapture data, "there is always the possibility of analyzing live recapture data by dead-recovery formulae." This is accomplished by ignoring all but the first and last capture occasions for each animal (Brownie *et al.*, 1978, p. 175).

One objective of this paper is to emphasize that this approach (e.g., Mardekian and McDonald, 1981) is now outdated. The appropriate methodology for multiple capture-recapture data has now been developed by Pollock (1981), Jolly (1982), and Crosby and Manly (submitted to *Biometrics*). Comprehensive

computer programs are now available. Jolly-Seber analyses (Jolly, 1965; Seber, 1965) can be performed using "POPAN" developed by Arnason and Baniuk (1978) or a program available from J. E. Hines and J. D. Nichols, U. S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20811. Hines and Nichols also have a program to carry out the analysis for the age-dependent version of the Jolly-Seber model.

Biologists should be made aware that use of the band-recovery models with live recapture data involves "throwing away" data, with consequent loss of efficiency. We show that the loss in efficiency for survival estimators can be substantial.

Recently, Nichols and Pollock (1983) and Conroy and Nichols (1984) have shown that capture-recapture and band-recovery methodology can be used in the analysis of fossil data. In that context, there are some data sets where only first and last capture information is available. Therefore, a second objective of this paper is to present new estimators and their standard errors, of capture probabilities and population sizes which will be useful to paleobiologists. We also show their loss in efficiency if complete history information were available. An example using real fossil data is presented, and finally, a general discussion is presented.

2. Experimental Situation

The situation considered is a capture-recapture study, described for example by Jolly (1965), Seber (1965), or Pollock (1981), involving multiple recaptures of uniquely marked animals. Of interest is the loss

in efficiency incurred by discarding intervening capture records and applying band-recovery analyses (e.g., Models 1 and H_1 in Brownie *et al.*, 1978) to the first and last captures only. The single age class situation (cf. Jolly, 1965; Seber, 1965) is considered first, and then two age classes (cf. Pollock, 1981).

For simplicity, it is assumed that there are no losses on capture. Otherwise, the usual assumptions are made that animals suffer independent fates, and that the population is homogeneous, at least within an age class, to time-specific survival and capture probabilities (see for example, Seber, 1982, p. 196).

3. One age Class

3.1 Notation

Notation used is, in general, consistent with that in Chapter 5 of Seber (1982). However, comparison between the multiple capture-recapture and band-recovery methods makes it necessary to extend this notation and achieve some compromise with that in Brownie *et al.* (1978).

For the single age class Jolly-Seber model described by Seber (1982, p. 196), the following notation is used.

- s is the number of sampling occasions.
- N_i is the total number in the population just before the i th sample, $i=1, \dots, s$.
- M_i is the number of marked animals in the population before the i th sample, $i=1, \dots, s$, $M_1 \equiv 0$.
- $U_i = N_i - M_i$, $i=1, \dots, s$.
- ϕ_i is the survival rate from i to $i+1$, $i=1, \dots, s-1$.
- $p_i = 1 - q_i$ is the probability an animal is captured in the i th sample given that it is present, $i=2, \dots, s$.
- u_i is the number first caught in the i th sample, $i=1, \dots, s-1$.
- m_i is the number of marked animals caught in the i th sample, $i=2, \dots, s$.
- R_i is the number of marked animals released after the i th sample, $i=1, \dots, s-1$. ($R_i = u_i + m_i$ assuming no losses on capture).
- r_i is the number of the R_i that are captured at least once after the i th sample, $i=1, \dots, s-1$.
- z_i is the number captured before and after, but not in, the i th sample, $i=2, \dots, s-1$.
- χ_i is the probability an animal present just after the i th sample is not captured again, and is represented recursively by

$$1 - \chi_i = \begin{cases} 0 & \text{if } i = s \\ \phi_i \{ (1 - \chi_{i+1}) + p_{i+1} \chi_{i+1} \} & i = 1, \dots, s-1 \end{cases}$$

In order to apply the band-recovery Model 1 analysis to the multiple recapture data, and obtain valid variance estimates, the recapture data are used to construct a recovery matrix. The number of new releases after sample i , u_i , and the number of this cohort last captured on each following sampling occasion are recorded in the i th row and appropriate columns of the recovery matrix (see, e.g., Mardekian and MacDonald, 1981; Conroy and Nichols, 1984). Entries in the recovery matrix are denoted r_{ij}^* , where r_{ij}^* is the number of the u_i first captured and released at the i th sample, that are recaptured for the last time in the j th sample, $i=1, \dots, s-1$, $j=i+1, \dots, s$ (see Table 1).

[Table 1]

As indicated in Table 1, summary statistics based on the recovery matrix $\{r_{ij}^*\}$ are

m_i^* , the number of marked animals recaptured for the last time in the i th sample, $i=2, \dots, s$.

r_i^* , the number subsequently recaptured of the u_i first captured in the i th sample, $i=1, \dots, s-1$,

and t_i^* , the number first captured before or in the i th sample and subsequently recaptured after the i th sample,

$i=1, \dots, s-1$ ($t_1^* = r_1^*$, $t_i^* = t_{i-1}^* + r_i^* - m_i^*$, $i > 1$).

The relationship between these statistics, m_i^* , r_i^* , t_i^* and C_i , R_i , T_i in the usual band-recovery formulation (Brownie *et al.*, 1978, p. 13) is not entirely straightforward, because release and recovery (recapture) in the same period occurs in the typical band-recovery study but cannot occur in the recapture studies considered here. Thus, the diagonal elements of the usual recovery matrix are missing in $\{r_{ij}^*\}$ and columns are shifted to the left.

3.2 Estimators and Large Sample Variances

Estimating survival rates is the main objective in many recapture studies, and is considered first. As noted by Seber (1982, p. 215), equivalent results are obtained if survival rate estimators and their large-sample variances are derived using a likelihood with the u_i (new releases at i) as random variables, or a likelihood conditional on fixed u_i . This is also true for estimators of capture probabilities. Thus, in comparing estimators of ϕ_i and ρ_i , for the multiple recapture data results are drawn from Jolly (1965), Seber (1965) (where the u_i are random) and from Brownie and Robson (1983) (u_i fixed); and for the first and last captures, analogy is made to the band-recovery methods (Brownie *et al.*, 1978, u_i fixed).

For the multiple recapture data, the Jolly-Seber estimators and large-sample variances are (e.g., Seber, 1982; Brownie and Robson, 1983):

$$\hat{\phi}_i = \frac{r_i}{R_i} \frac{1}{m_{i+1} + z_{i+1}} \left(m_{i+1} + \frac{R_{i+1} z_{i+1}}{r_{i+1}} \right) \quad i=1, \dots, s-2 \quad (1)$$

$$\text{Var}(\hat{\phi}_i) = \phi_i^2 \left\{ \frac{E(M_{i+1} - m_{i+1}) E(M_{i+1} + u_{i+1})}{M_{i+1}^2} \left(\frac{1}{E(r_{i+1})} - \frac{1}{E(R_{i+1})} \right) \right. \\ \left. + \frac{E(M_i - m_i)}{E(M_i + u_i)} \left(\frac{1}{E(r_i)} - \frac{1}{E(R_i)} \right) \right\} + \frac{\phi_i (1 - \phi_i)}{E(M_i + u_i)} \quad (2)$$

$$\text{Cov}(\hat{\phi}_i, \hat{\phi}_{i+1}) = -\phi_i \phi_{i+1} q_{i+1} \left\{ \frac{1}{E(r_{i+1})} - \frac{1}{E(R_{i+1})} \right\}$$

$$\hat{p}_i = \frac{m_i}{m_i + R_i z_i / r_i} \quad i=2, \dots, s-1 \quad (3)$$

$${}^1\text{Var}(\hat{p}_i) = p_i^2 q_i^2 \left\{ \frac{1}{E(r_i)} - \frac{1}{E(R_i)} + \frac{1}{E(m_i)} + \frac{1}{E(z_i)} \right\} \quad (4)$$

For the first and last capture data, the likelihood of the r_{ij}^* conditional on the u_i is obtained by noting that the $(r_{i,i+1}^*, \dots, r_{is}^*)$ are mutually independent multinomial vectors characterized by

$$E(r_{ij}^*) = u_i \phi_i \dots \phi_{j-1} p_j \chi_j \quad i=1, \dots, s-1, j=i+1, \dots, s.$$

¹Note that $\text{var}(\hat{p}_i)$ in Brownie and Robson, 1983, p. 453, is incorrect.

The correct variance is given here.

By analogy to $P[\{R_{ij}\}]$ in Brownie and Robson (1976, p. 307), the likelihood of $\{r_{ij}^*\}$ conditional on the u_i is

$$P[\{r_{ij}^*\}] = \prod_{i=1}^{s-1} \binom{u_i}{r_{i,i+1}^*, \dots, r_{is}^*} f_i^{m_i^*} \phi_i^{t_{i+1}^* - r_{i+1}^*} \chi_i^{u_i - r_i^*}$$

where

$$f_i = \phi_{i-1} p_i \chi_i, \quad i=1, \dots, s-1.$$

A minimal sufficient statistic is $(r_1^*, \dots, r_{s-1}^*, t_2^*, \dots, t_{s-1}^*)$, where r_i^* given u_i is Binomial $(u_i, 1-\chi_i)$, and m_i^* given t_{i-1}^* is Binomial $(t_{i-1}^*, \phi_{i-1} p_i \chi_i / (1-\chi_i))$. This leads to the maximum likelihood estimators $\widetilde{1-\chi}_i = (r_i^* / u_i)$, $\widetilde{\phi_{i-1} p_i \chi_i} = (m_i^* / t_{i-1}^*) (r_{i-1}^* / u_{i-1})$. Using the recursive relationship $1-\chi_i = \phi_i p_{i+1} \chi_{i+1} + \phi_i (1-\chi_{i+1})$ gives

$$\widetilde{\phi}_i = \frac{r_i^*}{u_i} \frac{u_{i+1}}{r_{i+1}^*} \frac{t_{i+1}^* - m_{i+1}^*}{t_i^*} \quad i=1, \dots, s-2 \quad (5)$$

$$\widetilde{p}_i = \frac{r_i^*}{u_i - r_i^*} \frac{m_i^*}{t_{i-1}^* - m_i^*} \quad i=2, \dots, s-1 \quad (6)$$

The large sample variances and relevant non-zero covariances are

$$\left. \begin{aligned} \text{Var}(\tilde{\phi}_i) &= \phi_i^2 \left\{ \frac{1}{E(r_i^*)} - \frac{1}{u_i} + \frac{1}{E(r_{i+1}^*)} - \frac{1}{u_{i+1}} + \frac{1}{E(t_{i-m_{i+1}}^*)} - \frac{1}{E(t_i^*)} \right\} \\ \text{Cov}(\tilde{\phi}_i, \tilde{\phi}_{i+1}) &= -\phi_i \phi_{i+1} \left\{ \frac{1}{E(r_{i+1}^*)} - \frac{1}{u_{i+1}} \right\} \end{aligned} \right\} \quad (7)$$

$$\text{Var}(\tilde{\rho}_i) = \rho_i^2 \left\{ \frac{1}{E(r_i^*)} + \frac{1}{u_i - E(r_i^*)} + \frac{1}{E(t_{i-1-m_i}^*)} + \frac{1}{E(m_i^*)} \right\} \quad (8)$$

The estimators based on first and last captures are denoted $\tilde{\phi}_i, \tilde{\rho}_i$ to distinguish them from the Jolly-Seber estimators $\hat{\phi}_i, \hat{\rho}_i$.

The estimator $\tilde{\rho}_i$ and its variance do not appear in earlier articles and are included here because of their importance in the context of the example in Section 5. Also important in this context is estimation of N_i (the population size at i), and we present below the appropriate estimator \tilde{N}_i and its variance. In deriving \tilde{N}_i and $\text{Var}(\tilde{N}_i)$, it is assumed that u_i is Binomial (U_i, ρ_i) and t_{i-1}^* is Binomial ($M_i, 1-q_i \chi_i$) with U_i and M_i fixed and unknown. Thus, $\text{Var}(\tilde{N}_i)$ as presented below is for fixed N_i , and is comparable to Jolly's $V(\hat{N}_i | N_i)$ (equation (28), Jolly, 1965).

$$\tilde{N}_i = \frac{u_i}{\tilde{\rho}_i} + \frac{t_{i-1}^*}{1-q_i \chi_i} = \frac{u_i}{r_i^*} \frac{t_{i-1}^* m_i^{-m_i^*}}{m_i^*} (u_i - r_i^* + m_i^*) \quad i=2, \dots, s-1 \quad (9)$$

$$\text{Var}(\tilde{N}_i) = N_i^2 \left\{ \frac{1}{E(r_i^*)} - \frac{1}{E(u_i)} + \frac{1}{E(t_{i-1-m_i}^*)} + \frac{1}{E(m_i^*)} + \frac{q_i \chi_i^{-(1-\chi_i)}}{E(u_i - r_i^* + m_i^*)} \right\} \quad (10)$$

3.3 Loss in Efficiency

The loss in efficiency due to using only the first and last captures was examined by comparing the appropriate asymptotic standard errors (se's), obtained from the variances in the preceding section. For $\tilde{\phi}_i$ and $\hat{\phi}_i$ the variances used include the component of variation due to viewing the number of marked animals surviving to $i+1$, of those present at i , as the outcome of a chance process (cf. Jolly, 1965; Seber, 1965; Brownie *et al.*, 1978), rather than a fixed quantity (cf. Pollock, 1981). It seems appropriate to include this component of variation because survival estimates are often used to make comparisons across locations, times or conditions, and given the same inherent chance of survival, actual survival will vary from one occasion to another. For comparing \tilde{N}_i and \hat{N}_i , variances used were conditional on fixed N_i , and therefore reflect sampling variation, but not variation due to viewing N_i as a random variable (cf. Section 3.2, Jolly, 1982).

Percent loss in efficiency for $\tilde{\phi}_i$ was calculated as $100[1 - \text{se}(\hat{\phi}_i) / \text{se}(\tilde{\phi}_i)]$, and analogously for \tilde{p}_i and \tilde{N}_i . For simplicity, the u_i were assumed equal ($u_i = u, i=1, \dots, s-1$), loss in efficiency being independent of u in this situation. Also, in each case considered, a common value was used for the ϕ_i and for the p_i ($\phi_i = \phi, i=1, \dots, s-1$, and $p_i = p, i=2, \dots, s$). The cases considered included values of ϕ and p likely to obtain in practice. For example, values between 50 and 65% for annual survival rates are typical for many banding studies, and the recapture data in Mardekian and MacDonald (1981) yield estimates \hat{p}_i in the 30 to 40%

range, while the example in Pollock (1981) yields \hat{p}_i greater than 80%.

For a given set of values of ϕ , p and s , loss in efficiency is not the same for each $\tilde{\phi}_i$, $i=1, \dots, s-2$ (or for each \tilde{p}_i , \tilde{N}_i). To summarize results, loss in efficiency was calculated for each $\tilde{\phi}_i$ and individual values averaged. These averages are presented in Table 2 for the estimators of survival and capture probabilities and population size.

[Table 2]

Examination of Table 2 shows that average loss in efficiency is considerably greater for \tilde{p}_i and \tilde{N}_i than for $\tilde{\phi}_i$. This seems reasonable, as intermediate captures have a more direct effect on estimates of corresponding p_i (and hence of N_i) than on estimates of survival in preceding periods. Loss in efficiency is seen to increase as p increases, and to a lesser degree, as ϕ or the number of capture occasions (hence the number of intermediate recaptures) increase. Note that for values of $p \geq .30$ (corresponding to data in Mardekian and MacDonald, 1981 and Pollock, 1981), the loss in efficiency is substantial.

In summarizing their results, biologists often report an average

survival rate (e.g., $\bar{\phi} = \frac{1}{s-2} \sum_{i=1}^{s-2} \hat{\phi}_i$) and a standard error based on

$$\text{Var}(\bar{\phi}) = \frac{1}{(s-2)^2} \left[\sum_{i=1}^{s-2} \text{Var}(\hat{\phi}_i) + 2 \sum_{i=1}^{s-3} \text{Cov}(\hat{\phi}_i, \hat{\phi}_{i+1}) \right]. \quad \text{We therefore}$$

examined the loss in efficiency of $\bar{\phi} = \frac{1}{s-2} \sum_{i=1}^{s-2} \tilde{\phi}_i$, as compared to $\bar{\phi}$, by calculating the appropriate standard errors using variance and covariance formulae in (2) and (7). For $\rho \leq .3$, results were essentially the same as for $\tilde{\phi}_i$ in Table 2. For $\rho \leq .8$, loss in efficiency tended to be less severe for the average, $\bar{\phi}$, than for the individual $\tilde{\phi}_i$ (30 to 40% as compared to 40 to 50%). This is because the negative correlation between survival estimators for adjacent years is smaller in absolute magnitude for the $\hat{\phi}_i$, than for the $\tilde{\phi}_i$, for large ρ .

We also compared asymptotic standard errors for $\tilde{\phi}_H = \sum_{i=1}^{s-2} w_i \tilde{\phi}_i$ and $\hat{\phi}_H = \sum_{i=1}^{s-2} v_i \hat{\phi}_i$, where the weights w_i and v_i are chosen to minimize the asymptotic variances of $\tilde{\phi}_H$ and $\hat{\phi}_H$, respectively (subject to $\sum w_i = 1$ and $\sum v_i = 1$). Thus, $\hat{\phi}_H$ is the "Hanover estimator" described by Jolly (1982). This comparison provides information concerning the relative efficiency of the two maximum likelihood estimators of a constant survival rate, ϕ , obtained assuming constant survival, and (i) applying the Model 2 analysis of Brownie *et al.* (1978) to the first and last captures, or (ii) applying Model B of Jolly (1982) to the complete recapture information (see Appendix 4, Jolly, 1982). Results for loss in efficiency for $\tilde{\phi}_H$ (relative to $\hat{\phi}_H$) were very similar to those for $\bar{\phi}$ (relative to $\bar{\phi}$) for all cases considered.

4. Two age Classes

In this section, we consider estimation of young and adult survival rates (ϕ_i^0 and ϕ_i^1 respectively) given recapture information recorded separately for individuals marked as young and as adults. Pollock (1981) provides the appropriate estimators, $\hat{\phi}_i^0$ and $\hat{\phi}_i^1$, which utilize all the recapture

information. By omitting all but the first and last captures, Model H_1 of Brownie *et al.* (1978) could also be used to obtain survival estimates, $\tilde{\phi}_i^0$ and $\tilde{\phi}_i^1$, and we are interested in the inefficiency of this latter procedure.

The relevant estimators and variances are not reproduced here. However, $\text{var}(\hat{\phi}_i^0)$ and $\text{var}(\hat{\phi}_i^1)$ in Pollock (1981) do not allow for a variable number of survivors at $i+1$ of the marked animals of appropriate age present just after sample i . Thus, $\text{var}(\hat{\phi}_i^0)$ and $\text{var}(\hat{\phi}_i^1)$ of Pollock (1981) were adjusted (by adding the appropriate Binomial variance) in order to make comparisons with $\text{var}(\tilde{\phi}_i^0)$ and $\text{var}(\tilde{\phi}_i^1)$ based on the band-recovery Model H_1 analysis of first and last captures.

Loss in efficiency for the estimators $\tilde{\phi}_i^0$ and $\tilde{\phi}_i^1$ is illustrated for the example in Pollock (1981). For this 4-year study on neck-collared young and adult giant Canada geese (*Branta canadensis maxima*), the recapture (i.e., resighting) rates were high (about 90 percent). Survival rate estimates and estimated asymptotic standard errors obtained using the method of Pollock (1981) on all recaptures, and using the Model H_1 band-recovery analysis on first and last captures, are presented in Table 3. No adjustment was made to correct for the neck-collar loss problem (see Pollock, 1981). The standard errors of $\hat{\phi}_i^0$ and $\hat{\phi}_i^1$ in Table 3 are substantially larger than those in Pollock (1981) because here they include the component of variation due to viewing the numbers of marked survivors as variables, not fixed quantities.

[Table 3]

Loss in efficiency in Table 3 was calculated as in Section 3.3, but using the estimated standard errors. The roughly 50% loss in efficiency shows the Model H_1 analysis to be clearly inferior in terms of precision of estimates.

5. Application to Fossil Data

Paleobiologists interested in examination of variation in extinction rates have made use of compilations of fossil records consisting of the periods of first and last encounters of the taxa of interest. This "stratigraphic range data" is analogous to capture-recapture data where records of first and last capture only are available.

In this setting, individuals correspond to species or taxa and a sampling occasion corresponds to a geologic period. The first (last) capture occasion is the earliest (latest) period in which the taxon is encountered in the fossil record, and therefore, r_{ij}^* is the number of taxa first recorded in period i and last encountered in period j . Survival from the midpoint of one period to the midpoint of the next (ϕ_i) is the complement of the extinction rate, the capture probability (p_i) is an "encounter probability" or the probability that a taxon is observed in a period given that it is extant during that period, and the population size (N_i) refers to the total number of taxa present.

Further discussion concerning the correspondence between this type of paleontological data and capture-recapture methodology (including validity of assumptions) is contained in Nichols and Pollock (1983) and Conroy and Nichols (1984). The estimation of ϕ_i by applying the

band-recovery methods of Brownie *et al.* (1978) is also described by these authors. In this context, inefficiency of the band-recovery analyses is not an issue because the complete capture information is not available. However, use of the estimators \tilde{p}_i and \tilde{N}_i [equations (6) and (9)] add substantially to the information resulting from the analyses described by these authors.

The estimators \tilde{p}_i can be used to examine the validity of the commonly made assumption that the encounter probabilities are approximately one. This assumption is the basis of many earlier analyses of similar data, and reported trends in extinction rates, which are dependent on this assumption, may be completely erroneous if the actual p_i are less than one and not constant.

An example for families in the phylum Mollusca follows. Numbers of first and last encounters for periods ranging from the lower Ordovician to the upper Permian, based on data in Sepkoski (1982), are presented in Table 4.

[Table 4]

Using program ESTIMATE to perform the band-recovery analysis of Brownie *et al.* (1978) produces estimates of ϕ_i (but not of p_i and N_i), and tests for the different models. The band-recovery Model 3 (constant survival and recovery) is not expected to hold in this context, because the χ_i , and hence, $f_i = \phi_{i-1} p_i \chi_i$, are not constant when ϕ and p are constant. Thus, it is not surprising that constant recovery is rejected for these data (chi square = 130.24 with 42 degrees of freedom for the test

of fit to Model 3, and chi square = 78.91 with 9 degrees of freedom for the test of Model 3 versus Model 2). Constant survival was rejected in favor of time-specific ϕ_i , which was also expected, because the geologic periods are known to vary in length (chi square = 24.43 with 8 degrees of freedom for the test of Model 2 versus Model 1). Fit to the model with time-specific survival and recovery was acceptable (chi square = 23.05 with 25 degrees of freedom for the test of fit to Model 1). Thus, estimates of ϕ_i , ρ_i and N_i were obtained using the Model 1 output and equations (5), (6) and (9). Extinction rates were calculated as $1-\tilde{\phi}_i$, with standard error given by $se(\tilde{\phi}_i)$ and were not adjusted for the differences in lengths of the geologic periods. Estimates and estimated standard errors are presented in Table 5.

[Table 5]

Due to the small sample sizes (small u_i , r_i^* and m_i^*), estimates have poor precision, and are greater than 100 percent for one $\tilde{\phi}_i$ and one $\tilde{\rho}_i$. Nevertheless, it seems clear that results do not support the assumption of ρ_i constant and close to 100 percent. Further inferences about the ρ_i could be based on "contrasts" among the $\tilde{\rho}_i$ by means of approximate Z-tests using the estimated large sample variances; or on tests concerning a model where constant ρ is built into the cell expectations, these tests being beyond the capabilities of program ESTIMATE.

b. Discussion

In examining the inefficiency of the practically expedient band-recovery analysis on a subset (first and last captures only) of the recapture data, we have ignored bias of the different estimators. This is because various bias-reducing corrections can be employed which do not affect asymptotic variances (cf. Seber, 1982, p. 204 and Brownie *et al.*, 1978, p. 16).

Inefficiency associated with band-recovery analysis of multiple recapture data was addressed in Brownie *et al.* (1978), but for a different implementation of the analysis. The recovery matrix was assumed to contain every recapture for an individual recorded in the same row of the matrix, so that the multinomial structure of elements in a row was lost. Applying the band-recovery analysis to such a recovery matrix will produce invalid (negatively biased) variance estimates, and is not recommended (see the last paragraph of Section 8.2, Brownie *et al.*, 1978). The results for loss in efficiency in Brownie *et al.* (1978) do not apply to the analysis of first and last captures considered here.

Results in Table 2 may be used to assess the inefficiency of a band-recovery analysis of first and last captures. In doing this, it is important to note that recovery rates \hat{f}_i produced by the band-recovery analysis underestimate capture probabilities p_i . Inefficiency in Table 2 is based on the value of p_i and not $f_i = \phi_{i-1} p_i \chi_i$. In live recapture studies, capture probabilities p_i will often be substantially larger than the 5 percent recovery rate of many band-recovery studies, and the additional effort involved in implementing the appropriate multiple-recapture analysis will be warranted.

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Table 1

*Recovery matrix for first and last captures,
with summary statistics, for a study with s=5*

Number of first Captures	Time of last capture				Row totals
	2	3	4	5	
u_1	* r_{12}	* r_{13}	* r_{14}	* r_{15}	* $r_1 = t_1$
u_2		* r_{23}	* r_{24}	* r_{25}	* r_2
u_3			* r_{34}	* r_{35}	* r_3
u_4				* r_{45}	* r_4
Column totals	* m_2	* m_3	* m_4	* $m_5 = t_4$	

Table 2

Average percent loss in efficiency for estimators

$\tilde{\phi}_i, i=1, \dots, s-2, \tilde{p}_i, i=2, \dots, s-1, \text{ and } \tilde{N}_i, i=2, \dots, s-1$

		p							
Estimator		.05	.10	.20	.30	.40	.50	.80	.90
$\phi = .65, s=5$	$\tilde{\phi}_i$	4.8	9.3	17.5	24.7	31.0	36.5	48.6	51.2
	\tilde{p}_i	7.3	14.2	26.5	37.4	47.0	55.7	78.1	85.7
	\tilde{N}_i	7.2	13.8	25.4	35.4	44.4	52.5	74.8	83.1
$\phi = .65, s=10$	$\tilde{\phi}_i$	5.7	10.9	20.1	27.8	34.4	40.1	52.8	55.9
	\tilde{p}_i	9.1	17.2	31.0	42.3	51.8	60.0	80.3	87.0
	\tilde{N}_i	8.9	16.6	29.2	39.4	48.1	55.7	76.3	84.0
$\phi = .50, s=5$	$\tilde{\phi}_i$	4.1	8.1	15.5	22.2	28.3	33.9	47.6	51.1
	\tilde{p}_i	5.9	11.5	22.0	31.7	40.6	49.0	72.9	81.9
	\tilde{N}_i	5.8	11.3	21.4	30.5	39.0	47.0	70.6	80.0
$\phi = .50, s=10$	$\tilde{\phi}_i$	4.5	8.8	16.6	23.7	30.0	35.8	49.9	53.7
	\tilde{p}_i	6.6	12.8	24.0	34.0	43.0	51.3	74.2	82.7
	\tilde{N}_i	6.6	12.5	23.2	32.5	41.0	48.8	71.6	80.7

Table 3

Comparison of precision of survival rate estimates based on (a) all captures or (b) first and last captures, for Canada geese neck collar study (Pollock, 1981)

Parameter	Method of Estimation		Loss in Efficiency for (b) relative to (a). (percent)
	(a) Pollock (1981) model with all recaptures Estimate* (st. error*)	(b) Model H ₁ (Brownie <i>et al.</i> , 1978) with first and last captures Estimate* (st. error*)	
ϕ_1^0	.57 (.0457)	.51 (.0867)	47
ϕ_2^0	.50 (.0398)	.44 (.0807)	51
ϕ_1^1	.72 (.0584)	.72 (.1259)	54
ϕ_2^1	.63 (.0422)	.63 (.1201)	65

*Not adjusted for neck-collar loss (see Pollock, 1981).

Table 4

Numbers of first and last encounters of families of Mollusca in stratigraphic series ranging
from Ordovician to Permian (from Sepkoski, 1982)

Period of first encounter [‡]	Number encountered for first time (u_i)	Period of Last Encounter [‡]										Row totals r_i^*
		$\theta(m)$	$\theta(u)$	$S(l-m)$	$S(u)$	$D(l)$	$D(m-u)$	$C(l)$	$C(u)$	$P(l)$	$P(u)$	
$\theta(l)$	62	18	10	4	1	1	6	2	0	2	4	48
$\theta(m)$	38		9	4	2	1	6	1	0	1	2	26
$\theta(u)$	17			3	2	1	0	0	1	1	1	9
$S(l-m)$	29				3	3	8	0	0	0	3	17
$S(u)$	11					1	4	1	1	1	0	8
$D(l)$	31						17	2	1	1	1	22
$D(m-u)$	54							1	1	1	2	5
$C(l)$	41								12	4	6	22
$C(u)$	32									5	7	12
$P(l)$	25										7	7
Column totals m_j^*		18	19	11	8	7	41	7	16	16	33	

[‡] θ = Ordovician, S = Silurian, D = Devonian, C = Carboniferous, P = Permian, l = lower, m = middle, u = upper.

Table 5

*Estimates and standard errors for extinction probabilities
(1- ϕ_i), encounter probabilities (p_i), and numbers of extant
families (N_i) for families in the phylum Mollusca
(for the data in Table 4)*

Period	$1-\tilde{\phi}_i$	Se($1-\tilde{\phi}_i$)	\tilde{p}_i	Se(\tilde{p}_i)	\tilde{N}_i	Se(\tilde{N}_i)
$\theta(\ell)$	0.293	0.121				
$\theta(m)$	0.146	0.232	1.300	0.596	73.1	20.0
$\theta(u)$	0.313	0.199	0.578	0.325	99.3	34.4
$S(\ell-m)$	0.318	0.170	0.445	0.228	124.8	44.7
$S(u)$	0.113	0.199	0.485	0.377	83.2	29.8
$D(\ell)$	-1.974	1.389	0.380	0.216	144.9	55.2
$D(m-u)$	0.866	0.062	0.161	0.086	616.4	309.3
$C(\ell)$	0.067	0.272	0.337	0.180	166.1	73.7
$C(u)$	0.171	0.341	0.320	0.153	180.0	69.6
$P(\ell)$			0.239	0.131	197.3	90.8